

Key species and properties for perturbations of food webs

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It is a challenge to predict the response of a large, complex system to a perturbation. Recent attempts to predict the behavior of food webs have revealed that the more complex the system, the more precisely the elements of the system must be measured. As a result, the amount of effort needed to understand a system grows quickly with its complexity. Here, we show that not all elements must be measured equally well, suggesting a more efficient allocation of effort to understanding complex systems is possible. We then develop an iterative technique to efficiently arrive at this solution. Finally, in our assessment of model food webs, we find that it is most important to precisely measure the mortality and predation rates of large, generalist, top predators. Prioritizing the study of such species will make it easier to understand the response of complex food webs to perturbations.

I. INTRODUCTION

Predicting the result of environmental perturbations, such as the arrival of new species or habitat change, is a major goal in ecology [1, 38]. What makes this challenging is the complex interconnected nature of ecological systems. In any densely-connected system, a perturbation of one element can percolate across the network of interactions. This is particularly true for the complex food webs that form the backbones of most ecosystems [27, 33, 34, 37]. Even perturbations acting only on a small subset of species may thus propagate through the network and lead to serious systemic changes [4, 9, 27, 31, 36, 45].

A central factor determining the response of a food web to perturbations is its topology, the precise map of predator-prey interactions. It has been shown that topological properties affect local and global dynamical stability [5, 6, 15, 28–30] and other notions of robustness such as the likelihood of secondary extinctions [7]. Often, the food web topology can indicate the relative importance of species for different applications [2, 19, 20, 26]. However, topology alone is generally not sufficient for reliable predictions [32]. For instance, measures taking into account the biomass flows between species correlate much better with the results of numerical simulations than do topological indices alone [21].

In addition to knowledge of the topology, an accurate prediction of the impact of perturbations requires information about underlying biomass flows and the control coefficients characterizing the nonlinearity of processes. Such parameters require extensive measurements and errors in their estimation quickly reduce the accuracy of predictions about how food webs respond to perturbations [33, 44].

A lack of precise information on biomass flows and control coefficients limits our ability to make precise predictions on the ultimate effect of perturbations. For instance, predictions for systems of more than 25 species

are practically impossible, unless very detailed information is available [35].

Here, we ask if food web responses to a perturbation are more sensitive to particular species or parameters. If we can identify such influential elements in advance, we should be able to make more precise predications about dynamics with a given effort in parameterization.

In this paper, we investigate the predictability of responses to perturbations in a broad class of food web models. Our results show that the different parameters of different species do not need to be measured with the same accuracy. We use analytical calculations and numerical demonstrations to show that it is possible to assign to each species a value that indicates the importance of precise knowledge about this species for the quality of the prediction. Furthermore, we demonstrate that this importance can be estimated reasonably well from imprecise information. Finally, we identify which of the parameters of these important species are crucial to the prediction of responses to perturbations.

The paper is structured as follows: We start in Section II by introducing a method for predicting the impact of given perturbations in a broad class of food web models. The method is illustrated in Section III with two examples. In Section IV, we then derive measures for species' influence on others and for their sensitivity to perturbations. In Section V, we test these predictions in a series of numerical experiments. The numerical results illustrate a feasible strategy for field studies, where mathematical analysis and experimental measurements are used to iteratively improve predictions. In Section VI, we use computer experiments and statistical association to determine which parameters and types of species are most important to measure.

II. IMPACT EVALUATION

Consider a biological system described by a set of state variables X_1, \dots, X_N denoting, for instance, the abundances of established species in a food web. The system is now subject to a perturbation that is characterized by another set of variables Y_1, \dots, Y_M , for instance denoting the abundances of newly arriving species.

We assume that, in the absence of the perturbation, the variables X_1, \dots, X_N are governed by a set of ordinary differential equations of the form

$$\frac{d}{dt}X_i = A_i(X_1, \dots, X_N, Y_1, \dots, Y_M), \quad (1)$$

where A_i is a function representing the *right-hand-side* of the differential equations. For instance, the generalized model for food webs [13] which we use below, describes the dynamics of the populations X_1, \dots, X_N by N differential equation of the form

$$\frac{d}{dt}X_i = G_i(X) + S_i(X_i) - L_i(X) - M_i(X_i), \quad (2)$$

where G_i , L_i , M_i , and S_i are unspecified functions describing, respectively, the gain by predation (G_i), the loss by predation (L_i), the loss due to natural mortality (M_i), and the gain by primary production (S_i) of the focal species.

Following Ref. 35, we consider the case where the unperturbed system resides in a stable equilibrium X^* and where the perturbation is characterized by a small and constant Y^* , such as a new species persisting at a low constant abundance in the ecosystem due to initially positive growth or constant influx.

Because the stationary abundance, X_i^* , of a given established species i is dependent on the new species Y^* , we can regard it as a function $X_i^* = X_i^*(Y^*)$. We can then define the impact $I_{i,j}$ of a perturbation variable Y_j^* on a resident species abundance X_i^* as the change of X_i^* per unit Y_j^* , i.e.

$$I_{i,j} = \left. \frac{\partial X_i^*}{\partial Y_j^*} \right|_0, \quad (3)$$

where we used $|_0$ to indicate that the derivative is evaluated in the limit of vanishing densities of the arriving species Y_j^* . In other words, the entries of the impact matrix $I_{i,j}$ state the loss of units of the established species i per unit of arriving species j that enters the system.

In simple models, the impact can be computed by first solving (1) for the stationary solution $X_i^*(Y^*)$ and subsequently computing the derivative in (3). However, for more than three species, the analytical computation of the stationary solution becomes prohibitively difficult. Furthermore, we seek a general solution, that does not depend on the functional forms in the model. For these reasons, the explicit computation of the stationary solution is not possible.

Computing the stationary solution can be avoided by recognizing that the stationary density of a resident species X_i^* can be considered as an implicit function that is defined as the solution of the stationarity condition $0 = A_i(X^*, Y^*)$. Using a corollary to the implicit function theorem [22], we can then write the impact matrix as

$$\mathbf{I} = -\mathbf{J}^{-1}\mathbf{K}, \quad (4)$$

where the superscript -1 indicates the matrix inverse. The matrix \mathbf{J} is the so-called Jacobian, which is defined as the derivatives of A_i with respect to the abundances of established species, i.e. $J_{i,j} = \partial A_i / \partial X_j|_*$. And, the matrix \mathbf{K} is a $N \times M$ defined by $K_{i,j} = \partial A_i / \partial Y_j|_*$, where $|_*$ indicates that the derivative is evaluated in the equilibrium under consideration. The matrix \mathbf{K} thus captures the direct impact of an arriving species on an established species, which is quantified by the reduction in production (or respectively increase in mortality) of the established species per unit of the arriving species. To establish \mathbf{K} prior to the arrival therefore requires information about the species the arriving species is likely to interact with.

In summary, (4) establishes a relationship between the direct proximal impact of the arriving species \mathbf{K} , the indirect ultimate impact \mathbf{I} and internal interactions among the established species \mathbf{J} . Beyond the example of perturbations caused by an arriving species, (4) applies to press perturbations on an established community in general. As a note of caution, we remark that this relationship holds up to linear order. The impact-approximation therefore remains valid only as long as the perturbation caused is reasonably small.

Explicitly, (4) means that we can obtain the ultimate impact matrix as a function of the Jacobian of the established community and the matrix of the direct perturbations. For instance, consider a perturbation due to a single new species of abundance Y_1^* arriving in a system of established species. Because there is only a single arriving species, the matrix \mathbf{K} is a vector. For each established species i , the entry K_i denotes the changes to its biomass intake and loss rates that are directly caused by the new species, e.g. by feeding or competition. The impact vector \mathbf{I} then describes the response of each species to this change induced by K as the perturbation propagates through the network.

In the equations above, we refer to the steady state of the system, which seems to imply that information about this state is required. However, relationship (4) remains valid independently of the specific steady state under consideration. When the matrices are evaluated, the steady state appears only in the Jacobian which contains elements of the form $J_{i,j} = \partial / \partial X_j (dX_i/dt)|_*$. For instance, in the generalized food web model, this leads to expressions such as $\partial G_i / \partial X_i|_*$. Because we cannot evaluate this expression without further assumptions, it is an unknown quantity. However, we note that for any specific system the expression is simply a number. In other

words, this means that the unknown derivatives appearing in the Jacobian constitute unknown parameters of the model.

So far, we have recognized that the unknown derivatives can be formally treated as unknown parameters of the model. However, as such, these parameters are hard to interpret and are thus not suitable for an ecological discussion of the results. We solve this problem by using a slightly different parametrization, which is obtained either by a special normalization procedure [13] or directly by the identity

$$\left. \frac{\partial G_i}{\partial X_i} \right|_* = \frac{G_i^*}{X_i^*} \left. \frac{\partial \log G_i}{\partial \log X_i} \right|_*, \quad (5)$$

which is true for $G_i^*, X_i^* > 0$ (a condition that is generally met by definition; see Ref. 23 for the special case of $X_i^* = 0$).

The expression on the right-hand-side of (5) is a product of two factors that have a direct interpretation in most applications. The first factor is a per-capita rate. Such rates have the dimension of inverse time and can be directly interpreted as characteristic turnover rates, in this case, as the per-capita growth rate of the members of species i by predation on other species.

The second factor in (5) is a logarithmic derivative. Such derivatives are also called elasticities and have been proposed originally in economic theory [18] and subsequently in metabolic control theory [8] and ecology [40, 43]. They can be estimated well from observational data and interpreted straightforwardly. For every power-law, $f(x) = Ax^p$, the logarithmic derivative is $\partial \log f / \partial \log x = p$, independently of A or x . Thus, for instance, any linear function has an elasticity of one regardless of the slope. For functions that are not power-laws the elasticity still provides an intuitive non-linear measure of the sensitivity in the steady state. For instance, for the well-known Holling type-II functional response the corresponding elasticity is 1 if evaluated in the linear regime and 0 at saturation.

In summary, the identity (5) allows one to break the partial derivative of the process in the steady state into two constant factors, describing the per-capita rate and the sensitivity of the process, respectively. These factors are, therefore, well-defined ecological parameters in their own right, which can be understood and discussed even if the steady state of the system is unknown. For food webs, this parametrization leads to the Jacobian matrix expressions given in A[13]. According to (4), the Jacobian that is thus parameterized can then be used to relate a perturbation to its eventual impact. In the following, we use this approach to discuss the prediction of the impact of perturbations on food webs. We have so far focused specifically on the arrival of new species. Let us however remark that the applicability of (4) is not limited to this case, but remains valid for all perturbations that can be quantified by a set of variables Y^* .

We note that the approach to impact taken in this paper is closely related to [35]. Our main methodolog-

Name	Interpretation	Value(s)
Scale parameters - defining the biomass flows in the steady state.		
α_i	Rate of biomass turnover in species i	(0,1]
$\beta_{i,j}$	Contribution of predation by i to loss rate of species j	[0,1]
$\chi_{i,j}$	Contribution of species i to the prey of species j	[0,1]
ρ_i	Fraction of growth in species i gained by predation	0 (producers) 1 (consumers)
$\tilde{\rho}_i$	Fraction of growth in species i gained by primary production	$1 - \rho_i$
σ_i	Fraction of mortality in species i resulting from predation	0 (top pred.) (0,1] (others)
$\tilde{\sigma}_i$	Fraction of mortality in species i not resulting from predation	$1 - \sigma_i$
Elasticities - Sensitivities of interactions to state variables.		
γ_i	Sensitivity of predation in species i to i 's prey density	[0.5,1.5]
$\lambda_{i,j}$	Exponent of prey switching	1 (passive)
μ_i	Exponent of closure in species i	[1,2]
ϕ_i	Sensitivity of primary production in species i to the density of species i	[0,1]
ψ_i	Sensitivity of predation in species i to the density of predators	[0.5,1.5]

TABLE I: Generalized model parameters as defined in Ref. 13.

ical contribution is to apply this approach to generalized models. The advantage of generalized modeling is its high numerical efficiency, which enables a detailed and statistically sound numerical exploration. For the practical application to real world food webs, generalized models offer additional advantages. In contrast to half-maximum concentrations and maximal growth rates used in conventional models, all parameters of the generalized model are defined in the state observed in nature. The parameters can therefore be measured directly without requiring a fitting procedure. Furthermore, the parameters are defined in such a way that their estimation from noisy data converges maximally fast [18, 25]. In practice, this should lead to a higher accuracy.

The formulation of the generalized model is straightforward. Based on the results of [13] even large models with tens of species can be set up in few hours. Using the equations derived here, the impact of different species can then be computed in seconds on a small laptop, using a simple algorithm [3]. Once the model has been set up, integration of new data requires entering new numerical values. The computation of impact and importance therefore presents only a small additional effort to the field work needed to measure parameters.

III. EXAMPLES

For illustration, we consider two examples, a simple predator-prey system and the 10-species food web shown in Fig. 1. While the predator-prey system is analytically tractable, the second example requires numerical calcu-

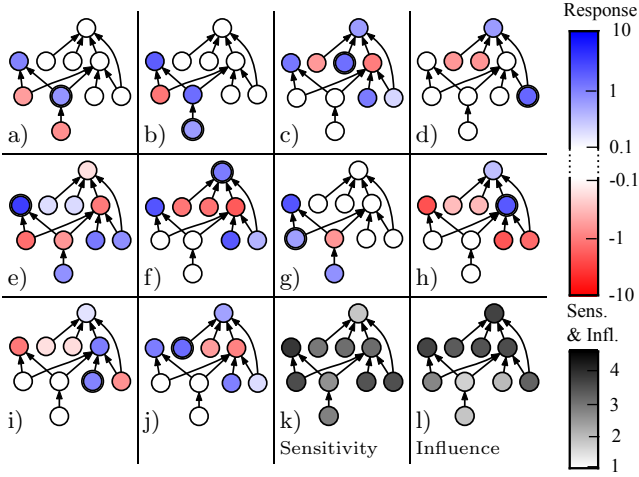


FIG. 1: Responses of a food web to perturbations of different species. Shown are species (circles) and predator-prey relationships (arrows, in the direction of the biomass flow). In a-j), the species represented as a thick-lined circle is affected by a perturbation that increases this species' biomass intake and thus leads to an increase in its abundance. The color code denotes the response of the system to this perturbation. The perturbation of each species i is normalized to the species turnover rate α_i , i.e. $K_i = \alpha_i$. In particular, the effect on the perturbed species is always positive, but the amount its abundance changes is determined by the surrounding system. In k) and l) the grey-scale denotes the sensitivity and the influence of each species respectively, approximating its propensity to experience or cause large impact (details are given in Section IV, or see C for their definitions (C3) and (C2)).

lations.

As a first example, we consider a class of predator-prey models in which a predator of abundance X_1 consumes a producer of abundance X_2 . A detailed treatment and discussion of the stability of this system in terms of the generalized model parameters can be found in Refs. 11, 13.

The Jacobian matrix of this system near the steady state is

$$\mathbf{J} = \begin{pmatrix} \alpha_1(\psi - \mu) & \alpha_1\gamma \\ -\alpha_2\sigma\psi & \alpha_2(\phi - \sigma\gamma - \tilde{\sigma}\mu) \end{pmatrix} \quad (6)$$

where α_i represents each species' turnover rate and σ the relative loss of the producer due to predation (instead of natural mortality). Furthermore, ϕ denotes the elasticity (i.e. sensitivity) of primary production to the producer abundance, γ the elasticity of predation to primary producer abundance, ψ the elasticity of predation to predator abundance, and μ the elasticity of natural mortality to a species' own abundance.

We now consider the impact of the arrival of a competing predator in the established producer-predator system. It can be assumed that this new predator has a direct negative effect on the primary producer but no direct effect on the established predator, such that the perturbation

matrix \mathbf{K} contains the entries $K_{1,1} = 0$ and $K_{2,1} < 0$. As shown in detail in B, the impact on the established predator is

$$I_1 = \frac{\alpha_1}{\det \mathbf{J}} \gamma K_2, \quad (7)$$

and the impact on the producer is

$$I_2 = \frac{\alpha_1}{\det \mathbf{J}} (\mu - \psi) K_2, \quad (8)$$

where $\det \mathbf{J} \geq 0$ represents the determinant of the Jacobian matrix.

We see that generally the impact on the established predator is negative. This result is intuitive as the established predator is now in exploitative competition with the arriving predator. Of particular interest is the case where the established predator suffers from linear loss ($\mu = 1$) and has an effect on the producer that scales linearly with the predator abundance ($\psi = 1$, i.e. there is no interference between the predators). In this limit, $\det \mathbf{J}$ approaches 0. For the impact on the producer, I_2 , the small denominator is compensated by $\psi - \mu$, which also vanishes [14]. However, the impact I_1 on the established predator approaches infinity. This is a manifestation of the well-known competitive exclusion principle, which precludes the coexistence of the predators in this case [12, 17]. The infinite value indicates that the impact of the arriving predator is disproportionately strong, because it leads to a loss of stability. Also in larger systems, such infinite values of the impact occur whenever the arrival of the new species causes the loss of local stability due to a bifurcation.

The assessment of impact in a larger food web can be carried out analogously, but requires numerical computations in which the generalized parameters are set to specific values. In the following, we consider generalized models described in detail in Ref. 15. The topology of a food web was generated using the niche model [41]. For this topology we then drew the generalized parameters uniformly and independently from the ranges given in Tab. I. A specific example of a food web in this family of models is shown in Fig. 1.

The panels in Fig. 1 show the response of the food web to the perturbation of different focal species. In the context of a newly arriving species, these perturbations represent the situation where the new species has a direct effect only on the one focal species. Perturbations of some focal species have greater impacts on the food web than others. For instance, in Fig. 1e) most species respond to the perturbation of the focal species while in Fig. 1a), few species respond to the perturbation of a different focal species.

IV. SENSITIVE AND INFLUENTIAL SPECIES

Now we identify two types of species that are particularly important for perturbations. *Sensitive species* are

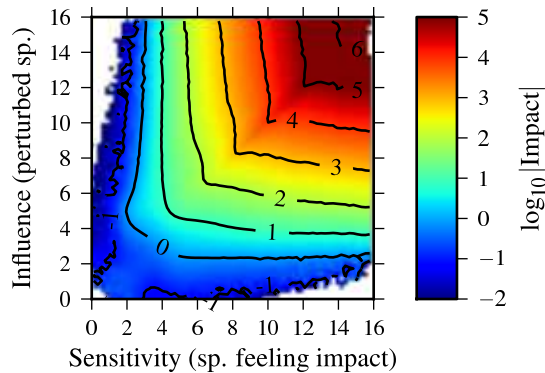


FIG. 2: The average absolute impact on a species with given sensitivity if a species of given influence is perturbed. The impact increases strongly with the influence of the perturbed species and with the sensitivity of the species feeling the impact. Parameters: System size $N = 50$, connectance $C = 0.04$.

easily perturbed by disturbances propagating through the web, and *influential species* have a strong effect on other species, when perturbed. In this section, we use intuitive reasoning to derive measures for the sensitivity and influence of each species. A more formal derivation is given in C.

Close to a steady state, the dynamical properties of a system are characterized by its dynamical modes which are characterized in terms of the eigenvectors and eigenvalues of the Jacobian matrix. For a given matrix, there are generally two different sets of eigenvectors, which are called right and left eigenvectors [42]. For each eigenvalue λ_k of the matrix there is a corresponding right eigenvector $v^{(k)}$ and left eigenvector $w^{(k)}$.

One can visualize dynamical modes as vibrations traveling through a drum when it is struck. Here the different modes correspond to different notes that are played on the drum. The right eigenvectors characterize the pattern of vibration when a specific note is played. Specifically, the elements of the right eigenvector describe how strongly the respective area of the drum vibrates in that note. The same is true for the food web. In a stable steady state that is hit by a short (pulse) perturbation the right eigenvectors govern how the system returns to the steady state after the perturbation.

Drummers know how to play different notes by striking different parts of the drum. This is captured by left eigenvectors. Specifically, the elements of the left eigenvector for a given dynamical mode describe how strongly the specific mode is excited when the drum is struck in a given area. Similarly, in the food web, the left eigenvectors characterize the strength of a specific dynamical response when a given species is perturbed.

Intuitively, one can think of each dynamical mode as a possible response of the system to a perturbation. More precisely, the right eigenvector denotes the impact of response (which species “feel the vibrations”), while the corresponding left eigenvector denotes the type of per-

turbation that can trigger a particular response (which species needs to be perturbed to “play a given note”). For instance, consider the pair of a right eigenvector $v = (1, 2)$ and a left eigenvector $w = (1, 0)$. If a perturbation affects only the first species, the direction of the system’s response due this dynamical mode is in the direction $(1, 2)$; i.e., the second species changes twice as much as the first.

The strength of a mode’s response is determined by its *excitability*. The excitability is for a given mode given by the corresponding eigenvalue $1/|\lambda_k|$ of the inverse Jacobian matrix \mathbf{J}^{-1} , which has the same eigenvectors as \mathbf{J} (see C for more details). Intuitively, the eigenvalue λ_k of a dynamical mode indicates a system’s resistance to a particular perturbation. The impact of such a perturbation is, therefore, inversely proportional to this resistance.

In the case presented here, we consider that a perturbation continuously excites the same dynamical modes (press perturbation). The impact is therefore the combined continuous excitation resulting from the perturbation of these dynamical modes.

The potential impact that a species feels due to a given dynamical mode is the product of the mode’s excitability and the component of the right eigenvector on this species. The potential impact from all modes is the sum over the contributions from the individual modes. We define the *sensitivity* of a species, denoted Se , as the logarithm of this potential impact, where the logarithm brings the numerical values into a more manageable range. For a more formal derivation, see C.

The potential impact that a species causes by exciting a given dynamical mode is the product of the mode’s excitability and the component of the left eigenvector on this species. The potential impact caused through all nodes is the sum over the excitations of the individual modes. Analogously to the sensitivity, we define the *influence*, denoted In , as the logarithm of this potential excitation. For a more formal derivation, see C.

For the example food web in Fig. 1, the sensitivity and influence of each node in the food web are shown in panels k) and l). Comparison with the impact for this food web confirms that sensitive nodes were often affected by the perturbations happening elsewhere and that direct perturbation of influential nodes had a strong effect on the network.

The close relationship between the sensitivity, the influence, and the impact is also confirmed in Fig. 2. On average, the impact of a perturbation on a species increases strongly with its sensitivity, and with the influence of the directly perturbed species.

Inspecting a series of sample food webs, we observe that the number of the very influential and very sensitive species in each food web is small. For instance, we find that on average for each web only 18% of all species lie in the upper 30% of the sensitivity or influence range for that web.

In summary, knowledge of the Jacobian of a specific

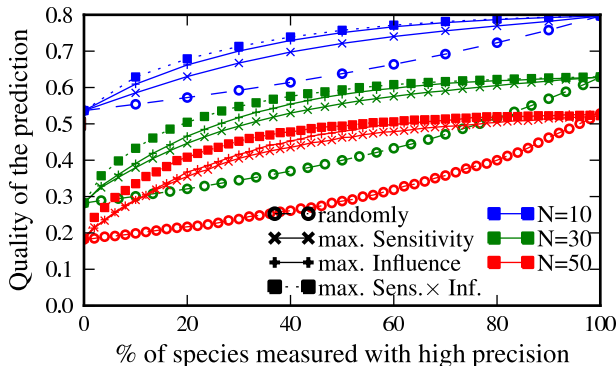


FIG. 3: Prediction quality when species are measured successively with higher precision. Starting on the left, all food web species are known with low precision. Advancing to the right the measurement error is reduced for one species at a time until all nodes have been measured with high precision. The different curves refer to different strategies for selecting the next species for improving precision. For the dashed line (empty symbols), the next species is selected randomly. For the solid curves, we first evaluate the sensitivity or influence of each species based on current knowledge and then select the species with the highest value of either sensitivity or influence. For the dotted curves we select the species with the highest product of influence and sensitivity ($Se_i In_i$). Error-carrying parameters of each node: $\alpha, \mu, \psi, \phi, \gamma, \sigma, \beta, \chi$. Other Parameters: Initial error of each parameter 10%, final error 2%, connectance $C = 0.04$.

food web enables us to predict the impact of specific perturbations, and also allows to gain a more general understanding of the species' sensitivity and influence with regard to perturbations of the network. The main challenge for impact assessment is thus to collect the necessary data for constructing the system's Jacobian. We show in the following that high precision is required only for some species.

V. ITERATIVE PARAMETER ESTIMATION

Intuitively, to understand the dynamics of a system, one would need accurate measurements of the properties of the most influential and sensitive species. However, our notion of sensitivity and influence is itself derived from the Jacobian matrix. Therefore, we can't identify the species that we need information from without having information on those species. We propose two ways to address this dilemma. In this section, we propose an iterative strategy in which existing preliminary information is used to estimate the impact and sensitivity of species. This preliminary assessment is then used to obtain improved parameter estimates on seemingly important species. Once additional data on these species becomes available, they can be used to further improve the estimates of the impact and sensitivity of species, re-

fining the process. Thus, a cycle is formed in which the necessary information for precise impact predictions is iteratively assembled.

We explore the quality of impact prediction in a series of numerical experiments. In each experiment, the task is to predict the impact of a random perturbation to a food web that was generated according to the procedure described in Sec. III. The food web generation determines values of the generalized parameters of the *true* Jacobian of the food web. In addition to this true Jacobian we generate an *estimated* Jacobian, in which we simulate measurement errors by drawing each generalized parameter from a log-normal distribution centered on the corresponding parameter value used in the true Jacobian. We then compute the true impact of the random perturbation, I based on the true Jacobian, and the estimated impact \tilde{I} based on the estimated Jacobian. The quality of the impact estimation is then evaluated as the cosine of the angle between the true and the estimated impact vector, which is computed as $Q = I \cdot \tilde{I} / (||I|| ||\tilde{I}||)$, where \cdot denotes the scalar product and $||I||$ is the norm of the vector I . The computation yields values between $Q = 1$, indicating an exact match of estimated and true impact, and $Q = -1$, indicating that the true impact for every species is the exact opposite of the prediction.

We now introduce a numerical implementation of the iterative strategy described above. We consider numerical experiments in which the knowledge of the Jacobian is initially poor, such that the generalized parameters are drawn from a lognormal distribution with a standard deviation of 10% of the true value. We furthermore assume that additional empirical work can be carried out on specific species that brings the error in all parameters of the respective species down to 2%. Our aim was to carry out the precise measurements in the order that leads to the most rapid increase in the quality of impact prediction.

For the purpose of demonstration, we consider four different protocols: a) precise measurements are carried out in random order, b) species are measured in the order of decreasing influence, c) species are measured in the order of decreasing sensitivity, d) species are measured in the order of the decreasing product of sensitivity and influence. The choice of species to measure next, was always based on the *estimated* Jacobian that is available at the time. Thus, only information is used that would also be available in the real world at the respective time.

The results shown in Fig. 3 demonstrate that estimating influence and sensitivity of the species prior to each measurement strongly increases the accuracy of predictions. This is particularly pronounced if measurements focus on the species with the highest product of sensitivity and influence. For instance, after measuring 20% of all species according to this protocol, we attain a quality of prediction comparable to measuring 60% – 80% of all species when species are chosen randomly. Using the estimation of influence and sensitivity to focus observational or experimental efforts can thus significantly reduce the amount of empirical work that is needed to

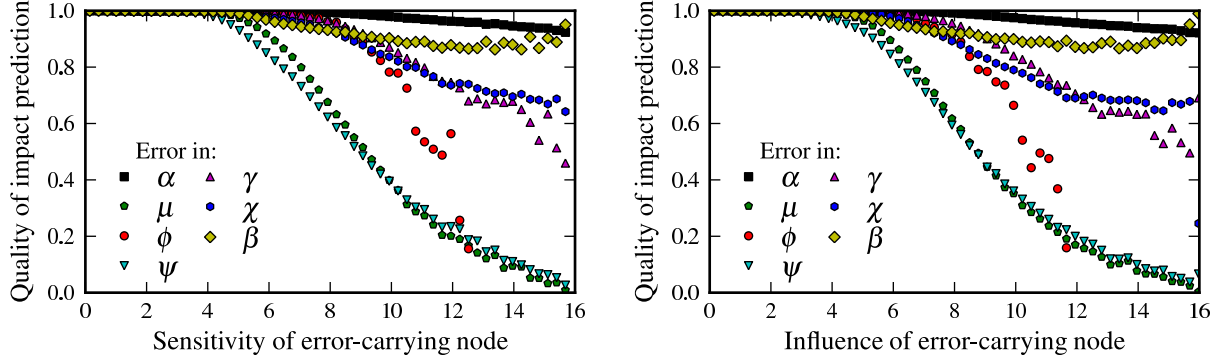


FIG. 4: Average quality of an impact prediction in the presence of measurement errors. The average quality of an impact prediction if one node with the specified sensitivity (left) or influence (right) in a food web is subject to a measurement error. The different datasets refer to errors in different parameters (c.f. Tab. I). Other parameters are: system size $N = 50$, connectance $C = 0.04$, and the standard deviation of the relative measurement error 10%. For higher C , the effect of χ and β increases (not shown). Noise around high importance and sensitivity values is due to the the relatively rare occurrence of these values in the numerical experiments.

achieve a given prediction quality.

VI. MOST IMPORTANT PARAMETERS AND SPECIES TO MEASURE

The iterative refinement procedure proposed above, needs some initial information on the system as a starting point. We therefore explore in this section, what types of parameters and what types of species were most important to measure.

To get an initial intuition of the importance of different parameters for impact prediction, we consider a situation where the estimated Jacobian is identical to the true Jacobian except for a single parameter that carries an error. Fig. 4 shows the quality of the estimated impact as a function of the influence and sensitivity of the species affected and the type of parameter varied. The figure furthermore shows the decrease in quality for sensitive and influential species depends on the parameter under consideration; precision in the elasticity of the mortality μ , and of the elasticity of predation ψ with respect to predator abundance were the most important. Fig. 4 thus confirms our intuition that not all parameters need to be measured to the same level of accuracy.

To determine which species are most important to measure in the absence of knowledge about the Jacobian, we look for simple correlations between sensitivity or influence and species properties (see below) in a set of 10^6 stable food webs. Each sample web consists of $N = 50$ species and has a connectance of 0.04. They are sampled by generating a niche model topology, then drawing the generalized parameters from uniform distributions in their ranges given in Tab. I, and retaining only stable configurations. For a given web, consider that each of the species i has a property x_i and sensitivity or influence y_i . Then we denoted the correlation coefficient between

x and y as $R = \sum_i (x_i - \bar{x})(y_i - \bar{y}) / \sqrt{x^2 y^2}$ where i runs over all species in a web, and where \bar{x} denotes the mean value of this property.

In the analysis, we consider the correlations (not causal effects) of sensitivity and influence with the following potential biological indicators:

- Generality, or the number of prey species of the focal species.
- Vulnerability, or the number of predators of the focal species.
- A binary value that is 1 if the focal species is a primary producer and 0 otherwise.
- The trophic level TL , which we calculate by solving a set of linear equations, such that $TL_i = 1$ for primary producers and $TL_i = 1 + \text{mean}(TL_{\text{prey}})$ for consumers, where $\text{mean}(TL_{\text{prey}})$ denotes the mean trophic level of i 's prey.
- The biomass turnover rate (generalized model parameter α), indicating the amount of biomass an individual consumes in comparison to its own mass.
- The network degree of a species, i.e. the total number of direct feeding interactions with other species.
- The weighted topological importance of a species WI^s as introduced in detail in 20. For each species, the value of WI^s indicates the indirect interactions from other species, based on the topology and biomass flows of a food web. The step parameter s indicates the maximum number of direct interactions, through which indirect effects are perceived. For instance, for $s = 2$, only effects on a species are considered from species that have a common prey or predator.

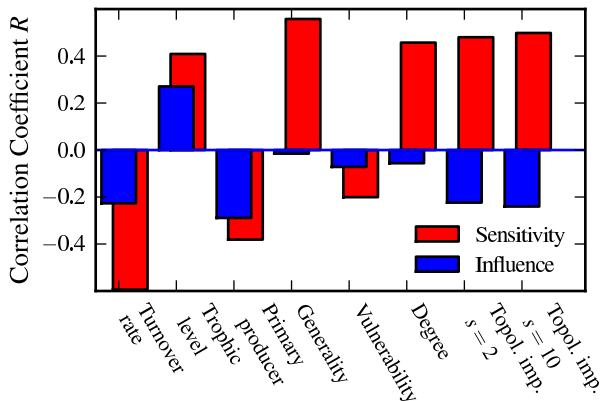


FIG. 5: Correlations of species' properties with their sensitivity and influence. The pattern of correlations is consistent with large predators playing an important role for a system's response to perturbations.

The correlation analysis, presented in Fig. 5, shows that high trophic levels and low biomass turnover rates correlate strongly with sensitivity and influence. This result suggests that top predators and other large species, despite their typically small total biomass, play a disproportionate role in the systems' response to perturbations. Without specific information on biomass flows, these are the species that should be targeted for initial parameterization.

The sensitivity of a species is highly correlated with its generality, while its influence appears to be independent. Intuitively, this might mean that a species with a large number of prey is likely affected if any of its prey species changes, while a perturbation of this species has little effect on each of the prey species.

The weighted topological importance correlates strongly with sensitivity and weakly with influence. This might mean that indirect effects influence how perturbation affect a species. However, the indirect effects from distant species had little effect.

In summary, high trophic levels and low biomass turnover rates correlate strongly with sensitivity and influence, while generality and large indirect effects correlate only with sensitivity. However, determining whether these correlations are causal requires statistical analyses beyond the scope of this paper.

VII. CONCLUSIONS

Previous work has suggested that without near perfect information on a range of parameters, it may be intractable to predict the effects of perturbances to large, complex systems [35]. In this paper, we proposed a method to predict the impact of perturbations on complex systems more efficiently. We used this method to investigate the relative importance of different species in

food webs. Our results show that there are typically a small number of species that are highly important, because they react sensitively to perturbations, have a strong influence on others, or both.

While we have focused exclusively on food webs, we note that the same approach can likewise be applied to other networks of nonlinear interactions that are found in metabolism [39], gene regulation [10], and cellular population dynamics [46].

Our results suggest that the potential impact of environmental perturbations on food webs can be predicted with reasonable accuracy if the most relevant parameters for only a small number of important species in the web are measured well. We have shown how to find these species iteratively, and how to pre-select potentially important species based on their biological properties. In addition, we have identified the parameters that are particularly important to measure accurately.

For real world food webs, identifying important species requires some initial information about the system. However, we demonstrated in numerical experiments that an iterative approach is feasible where preliminary inaccurate information is used to estimate the importance of different species, which can then be used to guide further field work, leading to refined predictions. Computing the importance of species based on a generalized model[13] can be done in seconds, even for large systems with tens of species, by using a simple algorithm [3].

Our correlation analysis suggests that it is most important to obtain precise parameter estimates for large, generalist consumers at top trophic levels. This analysis was not meant to determine which factors cause a species to be influential in a food web. Many of the biological traits we measured are highly correlated, and parsing out their independent effects was not a goal of our study. One could investigate hypotheses about biological traits that lead species to be more sensitive or influential in a food web, but that would require a different statistical approach than used here and is best the subject of future work.

Acknowledgments

We thank Prof. Mark Novak for discussions.

Appendix A: Generalized model Jacobian matrix

In this appendix, we show the explicit expressions of the Jacobian matrix for general food webs of the form(1) [13]. The diagonal and off-diagonal entries of the Jacobian depending on the generalized parameters in Tab. I

are separately given by

$$\begin{aligned}
J_{i,i} &= \alpha_i \left(\tilde{\rho}_i \Phi_i + \rho_i (\gamma_i \chi_{i,i} \lambda_{i,i} + \Psi_i) \right. \\
&\quad \left. - \tilde{\sigma}_i \mu_i - \sigma_i \left(\sum_k \beta_{k,i} \lambda_{k,j} ((\gamma_k - 1) \chi_{k,i} + 1) \right) \right) \\
J_{i,j} &= \alpha_i \left(\rho_i \gamma_i \chi_{i,j} \lambda_{i,j} \right. \\
&\quad \left. - \sigma_i \left(\beta_{j,i} + \sum_k \beta_{k,i} \lambda_{k,j} ((\gamma_k - 1) \chi_{k,j}) \right) \right).
\end{aligned}$$

Intuitively, the terms in the first line of each expression result from biomass intake, either by primary production of the focal species i ($\tilde{\rho}_i = 1, \rho_i = 0$) or from feeding on a species j ($\tilde{\rho}_i = 0, \rho_i = 1, \chi_{i,j} \neq 0$). The expressions in the second line of each expression are due to the loss of the focal species i either by natural mortality ($\tilde{\sigma}_i \mu_i$) or predation by species j ($\beta_{j,i} \neq 0$). The sums over k translate the indirect effects of apparent competition if i and j share a predator k . For a more detailed discussion, please refer to Ref. 13.

We note that \mathbf{J} characterizes the dynamics near any steady state. Stability of any particular steady state (corresponding to a particular set of generalized parameters) is ensured by checking that all eigenvalues of the Jacobian have negative real parts [16, 24].

Appendix B: Predator-prey example

In this appendix we provide the explicit calculations of the simple producer-grazer example. In this system, a grazer of biomass density X_1 consumes a primary producer of biomass density X_2 . The Jacobian matrix near the steady state is

$$\mathbf{J} = \begin{pmatrix} \alpha_1(\psi_1 - \mu_1) & \alpha_1 \gamma_1 \\ -\alpha_2 \sigma_2 \psi_1 & \alpha_2(\phi_2 - \sigma_2 \gamma_2 - \tilde{\sigma}_2 \mu_2) \end{pmatrix}. \quad (\text{B1})$$

A discussion of stability of this system in terms of the generalized modelling parameters can be found in Refs. 11, 13.

For calculating the impact of a given perturbation for each of the two species, we require the inverse of the Jacobian

$$\mathbf{J}^{-1} = \frac{1}{\det \mathbf{J}} \begin{pmatrix} \alpha_2(\phi_2 - \sigma_2 \gamma_2 - \tilde{\sigma}_2 \mu_2) & -\alpha_1 \gamma_1 \\ \alpha_2 \sigma_2 \psi_1 & \alpha_1(\psi_1 - \mu_1) \end{pmatrix}, \quad (\text{B2})$$

where

$$\det \mathbf{J} = \alpha_1 \alpha_2 (\phi_2 - \sigma_2 \gamma_2 - \tilde{\sigma}_2 \mu_2) (\psi_1 - \mu_1) \quad (\text{B3})$$

denotes the determinant of \mathbf{J} .

As a perturbation, we now consider a new grazer that has a direct negative effect on the primary producer, but

no direct effect on the established grazer. The perturbation K is therefore given by $K_1 = 0, K_2 < 0$. Now we plug this vector K in the impact equation (4) to obtain $I = -\mathbf{J}^{-1}(0, K_2)^T$. The impact on the grazer, I_1 , and the impact on the producer, I_2 are therefore

$$I_1 = \frac{\alpha_1}{\det \mathbf{J}} \gamma_1 K_2 \quad \text{and} \quad I_2 = \frac{\alpha_1}{\det \mathbf{J}} (\mu_1 - \psi_1) K_2. \quad (\text{B4})$$

Appendix C: Derivation of influence and sensitivity

Here, we derive the expressions for the influence and sensitivity of the food web species that are motivated in the paper with intuitive arguments. For this, we decompose the Jacobian matrix into the dynamical modes of the system. Then we use the impact-definition in (4) to identify sensitive species as those for which the expected impact of randomly excited modes is largest, and to identify influential species as those for which the expected excitation of dynamical modes is largest when they are perturbed.

Each dynamical mode of the Jacobian matrix consists of a left eigenvector $w^{(k)}$, a right eigenvector $v^{(k)}$ and a corresponding eigenvalue λ_k . Writing all the right eigenvectors as the columns of the matrix results in the transformation matrix $\mathbf{V} = (v^{(1)} \dots v^{(N)})$. For the left eigenvectors we analogously obtain the matrix \mathbf{W} . In terms of these matrices, and of the diagonal matrix \mathbf{D} containing the eigenvalues of \mathbf{J} , we can write $\mathbf{J} = \mathbf{VDW}^T$.

The inverse Jacobian matrix \mathbf{J}^{-1} , required for the impact calculation, has the same the same right and left eigenvectors $v^{(k)}$ and $w^{(k)}$ as the Jacobian matrix, corresponding to the eigenvalues $1/\lambda_k$. Therefore \mathbf{J}^{-1} can be written as $\mathbf{J}^{-1} = \mathbf{VD}^{-1}\mathbf{W}^T$.

Now we insert $\mathbf{J}^{-1} = \mathbf{VD}^{-1}\mathbf{W}$ into the impact equation (4). For a given perturbation vector K the impact is then

$$I = \sum_k v^{(k)} \frac{w^{(k)} \cdot K}{\lambda_k}, \quad (\text{C1})$$

where k runs over all eigenvalues and where \cdot denotes the scalar product. Impact is thus the sum over the dynamical modes of the Jacobian matrix.

We see that for a given mode k in (C1) the contribution to the impact on a given node depends on three factors. First, the product $w^{(k)} \cdot K$ determines which dynamical modes are excited by the perturbation. Second, $v^{(k)}$ determines which entries in I are affected by this dynamical mode. And finally $1/\lambda_k$ indicates how strongly the mode will be excited.

For the sensitivity of a species, we do not want to explicitly refer to any particular perturbation K . In absence of additional information, we therefore consider the case of a perturbation affecting every dynamical mode k with identical probability. The sensitivity Se_i can thus

be measured as the effects on node i ,

$$\text{Se}_i = \log \left(\sum_k \frac{|v^{(k)}_i|}{|\lambda_k|} \right), \quad (\text{C2})$$

where $|v^{(k)}_i|$ denotes the absolute value of $v^{(k)}$ on node i , and where we used the logarithm to bring the numerical values into a more manageable range.

For the influence of a species, we evaluate the impact

of a perturbation affecting only this specific species K . In absence of additional information, the influence is measured by the resulting excitation of all the dynamical modes

$$\text{In}_i = \log \left(\sum_k \frac{|v^{(k)}_i|}{|\lambda_k|} \right). \quad (\text{C3})$$

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- [1] P. A. Abrams. Evolution and the consequences of species introductions and deletions. *Ecology*, 77(5):1321–1328, July 1996.
 - [2] S. Allesina and A. Bodini. Who dominates whom in the ecosystem? energy flow bottlenecks and cascading extinctions. *Journal of Theoretical Biology*, 230(3):351–358, Oct. 2004.
 - [3] H. Aufderheide. CIP - calculator for the impact of perturbations. <http://www.biond.org/content/download>, Jan. 2013.
 - [4] M. Clavero and E. Garcia-Berthou. Invasive species are a leading cause of animal extinctions. *Trends in ecology and evolution*, 20(3):110–110, 2005.
 - [5] J. M. Dambacher, H. W. Li, and P. A. Rossignol. Relevance of community structure in assessing indeterminacy of ecological predictions. *Ecology*, 83(5):1372–1385, May 2002.
 - [6] J. M. Dambacher, H. Luh, H. W. Li, and P. A. Rossignol. Qualitative stability and ambiguity in model ecosystems. *The American Naturalist*, 161(6):876–888, June 2003.
 - [7] J. A. Dunne, R. J. Williams, and N. D. Martinez. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5(4):558–567, 2002.
 - [8] D. A. Fell. Metabolic control analysis: a survey of its theoretical and experimental development. *Biochemical Journal*, 286(2):313–330, 1992.
 - [9] D. F. Fraser and J. F. Gilliam. Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ecology*, 73(3):959–970, 1992.
 - [10] E. Gehrman and B. Drossel. Boolean versus continuous dynamics on simple two-gene modules. *Physical Review E*, 82(4):046120, Oct. 2010.
 - [11] T. Gross, W. Ebenhöf, and U. Feudel. Enrichment and foodchain stability: the impact of different forms of predator–prey interaction. *Journal of Theoretical Biology*, 227(3):349–358, Apr. 2004.
 - [12] T. Gross, A. M. Edwards, and U. Feudel. The invisible niche: Weakly density-dependent mortality and the coexistence of species. *Journal of Theoretical Biology*, 258(1):148–155, May 2009.
 - [13] T. Gross and U. Feudel. Generalized models as a universal approach to the analysis of nonlinear dynamical systems. *Phys. Rev. E*, 73(1):16205, 2006.
 - [14] T. Gross and U. Feudel. Local dynamical equivalence of certain food webs. *Ocean Dynamics*, 59(2):417–427, 2009.
 - [15] T. Gross, L. Rudolf, S. A. Levin, and U. Dieckmann. Generalized models reveal stabilizing factors in food webs. *Science*, 325(5941):747–750, Aug. 2009.
 - [16] J. Guckenheimer and P. Holmes. *Nonlinear oscillations, dynamical systems, and bifurcations of vector fields*. Springer, 2002.
 - [17] G. Hardin. The competitive exclusion principle. *Science*, 131(3409), 1960.
 - [18] H. S. Houthakker and S. P. Magee. Income and price elasticities in world trade. *The Review of Economics and Statistics*, 51(2):111–125, May 1969.
 - [19] F. Jordán. Keystone species and food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1524):1733–1741, June 2009.
 - [20] F. Jordán, W.-c. Liu, and A. J. Davis. Topological key-stone species: measures of positional importance in food webs. *Oikos*, 112(3):535–546, 2006.
 - [21] F. Jordán, T. A. Okey, B. Bauer, and S. Libralato. Identifying important species: Linking structure and function in ecological networks. *Ecological Modelling*, 216(1):75–80, Aug. 2008.
 - [22] H. Khalil and J. Grizzle. *Nonlinear Systems*. Macmillan Publishing Company New York, 2 edition, 1992.
 - [23] C. Kuehn, S. Siegmund, and T. Gross. Dynamical analysis of evolution equations in generalized models. *IMA Journal of Applied Mathematics*, May 2012.
 - [24] Y. A. Kuznétsov. *Elements of applied bifurcation theory*, volume 112 of *Applied Mathematical Sciences*. Springer Verlag, 1998.
 - [25] S. J. Lade and T. Gross. Early warning signals for critical transitions: A generalized modeling approach. *PLoS Comput Biol*, 8(2):e1002360, Feb. 2012.
 - [26] S. Libralato, V. Christensen, and D. Pauly. A method for identifying keystone species in food web models. *Ecological Modelling*, 195(3–4):153–171, June 2006.
 - [27] M. C. Mack and C. M. D’Antonio. Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution*, 13(5):195–198, May 1998.
 - [28] N. D. Martinez. Artifacts or attributes? effects of resolution on the little rock lake food web. *Ecological Monographs*, 61(4):367–392, 1991.
 - [29] R. M. May. Qualitative stability in model ecosystems. *Ecology*, 54(3):638–641, May 1973.
 - [30] K. S. McCann. The diversity–stability debate. *Nature*, 405(6783):228–233, May 2000.
 - [31] B. A. Menge. Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. *Ecological Monographs*, 65(1):21–74, Feb. 1995.
 - [32] L. S. Mills, M. E. Soulé, and D. F. Doak. The keystone-species concept in ecology and conservation. *BioScience*, 43(4):219–224, Apr. 1993.

- [33] J. Montoya, G. Woodward, M. C. Emmerson, and R. V. Solé. Press perturbations and indirect effects in real food webs. *Ecology*, 90(9):2426–2433, Aug. 2009.
- [34] H. A. Mooney and E. E. Cleland. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, 98(10):5446, 2001.
- [35] M. Novak, J. T. Wootton, D. F. Doak, M. Emmerson, J. A. Estes, and M. T. Tinker. Predicting community responses to perturbations in the face of imperfect knowledge and network complexity. *Ecology*, 92(4):836–846, 2011.
- [36] I. Parker, D. Simberloff, W. Lonsdale, K. Goodell, M. Wonham, P. Kareiva, M. Williamson, B. Von Holle, P. Moyle, J. Byers, and L. Goldwasser. Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, 1(1):3–19, 1999.
- [37] M. Pascual and J. A. Dunne. *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press, Dec. 2005.
- [38] A. K. Sakai, F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O’Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. The population biology of invasive species. *Annual Review of Ecology and Systematics*, 32, 2001.
- [39] R. Steuer, T. Gross, J. Selbig, and B. Blasius. Structural kinetic modeling of metabolic networks. *PNAS*, 103(32):11868, 2006.
- [40] D. Stiefs, G. A. K. van Voorn, B. W. Kooi, U. Feudel, and T. Gross. Food quality in producer-grazer models. *Am. Nat.*, 176:367–380, 2010.
- [41] R. J. Williams and N. D. Martinez. Simple rules yield complex food webs. *Nature*, 404(6774):180–183, 2000.
- [42] S. S. M. Wong. *Computational Methods in Physics and Engineering (2nd Edition)*. World Scientific, 1997.
- [43] J. Yeakel, D. Stiefs, M. Novak, and T. Gross. Generalized modeling of ecological population dynamics. *Theoretical Ecology*, 4(2):179–194, 2011.
- [44] P. Yodzis. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology*, 69(2):508–515, 1988.
- [45] T. M. Zaret and R. T. Paine. Species introduction in a tropical lake a newly introduced piscivore can produce population changes in a wide range of trophic levels. *Science*, 182(4111):449–455, Nov. 1973.
- [46] M. Zumsande, D. Stiefs, S. Siegmund, and T. Gross. General analysis of mathematical models for bone remodeling. *Bone*, 48(4):910–917, Apr. 2011.

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